Assessing the stock status of holobenthic octopus fisheries: is catch per unit effort sufficient?

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Holobenthic and merobenthic octopus fisheries are commonly treated as biological equivalents, regardless of their contrasting life-history strategies. This is the consequence of a lack of species identification and relevant biological information for many species, which has led to a reliance on catch per unit effort (cpue) data for stock status assessments. Using the commercial *Octopus pallidus* fishery in southeast Australian waters as a case study, the reliability of commercial cpue data as an indicator of stock status for holobenthic octopus fisheries was assessed. To achieve this, cpue and biological information from a fixed position experimental research line were investigated for consistency in stock status patterns and compared with commercial fishery cpue trends. Research line results revealed that cpue could remain stable regardless of size-selective fishing mortality potentially impacting recruitment. The cpue in the commercial fishery was very seasonal and dominated by females during autumn, when both cpue and spawning periods peaked, so increasing the potential for negative fishery impacts on egg production. The inability of cpue to account for the effects of continual fishing pressure on recruitment or seasonal changes in sex-specific catchability, however, indicates that cpue alone cannot provide sufficient information on the status of a holobenthic octopus fishery.

Keywords: catch per unit effort, effects of fishing, octopus, recruitment, season.

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Introduction

Most octopus species are regarded as short-lived and fast-growing ecological opportunists (Rodhouse and Nigmatullin, 1996; Moltschaniwskyj, 2004; Boyle and Rodhouse, 2005) that are more resilient to fishing pressure than many teleosts (Caddy and Rodhouse, 1998). This view, coupled with a general decline in the catch rates of many marine taxa, has contributed to a global increase in octopus catches of more than 100 000 t over the past two decades to 350 000 t in 2005 (FAO, 2005). However, the resilience of octopus stocks as a whole to increased fishing pressure is generally unknown, because most octopod research has concentrated on the small number of species that constitute most of the world's octopus catch, i.e. *Octopus vulgaris* (Quetglas *et al.*, 1998), *Octopus mimus* (Rocha and Vega, 2003), and *Enteroctopus dofleini* (Hartwick *et al.*, 1988). Those species are merobenthic, producing hundreds of thousands of eggs and planktonic hatchlings. In contrast, many other commercially exploited octopus species, which are harvested at relatively low levels, are afforded minimal research and management priority, and often categorized as unspecified "octopus" or bycatch in commercial logbook returns (Rocha and Vega, 2003; Boyle and Rodhouse, 2005). A large proportion of these lesser-known octopus species are holobenthic, i.e. they produce egg batches in the hundreds, and benthic hatchlings (Roper *et al.*, 1984).

Applying fisheries management strategies suitable for merobenthic octopus to the management of holobenthic octopus fisheries could jeopardize their sustainability. Recruitment dynamics for holobenthic species appear to be much more localized than for merobenthic species and are more likely to be dependent on the local population (Narvarte *et al.*, 2006). This suggests that if a localized area is subjected to continuous fishing pressure, the impact on recruitment for that area could be greater for holobenthic than for merobenthic octopus species (Boletzky, 2003). However, the potentially different impacts of fishing pressure on recruitment of holobenthic and merobenthic octopus may not necessarily be identifiable in fisheries data, where catch per unit effort (cpue) information is commonly used as the primary stock status predictor (Defeo and Castilla, 1998; Tsangridis *et al.*, 2002). This is because of the general patchiness and high turnover rates of octopus populations (Diallo *et al.*, 2002) combined with a lack of species identification (Boyle, 1990; Rocha and Vega, 2003).

Octopus pot fisheries operate by providing refuges in typically habitat-limited sandy substrata. Adults dominate catches, and pots are often used by females to brood eggs (Faraj and Bez, 2007). The removal of brooding females in a pot fishery could intensify any localized impacts on recruitment, particularly of holobenthic species, owing to the limited dispersal of juveniles. Such localized impacts on stock and recruitment have been suspected in the pot fishery targeting the holobenthic *Octopus pallidus* in the waters of the Bass Strait off Tasmania, southeast Australia (Figure 1). Established in 1981, the *O. pallidus* fishery (OPF) is a small, single-company fishery that operates two full-time vessels. The OPF is

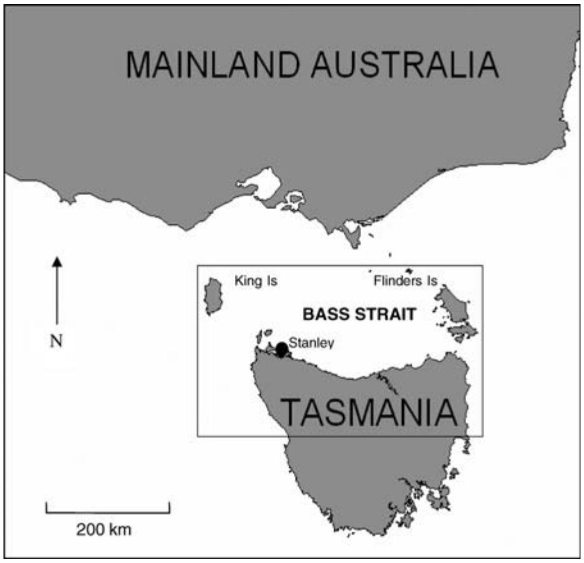

Figure 1. Extent of the OPF area (black square) and location of the research line (black dot) in Southeast Australian waters.

one of the few expanding fisheries in Tasmania (Ziegler *et al.*, 2007), with increasing catches, exploration of new fishing grounds, and significant investment in new vessels and processing plant infrastructure. The octopuses are caught in moulded plastic pots (volume 3000 ml) attached to demersal longlines 3–4 km long and set at variable depths of 15–85 m. Annual catches have risen from 18 t in 1991 to 77 t in 2007, peaking at 95 t in 2005 (Figure 2a). Since 1998, the OPF has been managed using gear restrictions, with a limit of 20 000 pots. However, in 2006, a total allowable catch of 100 t in the historically heavily fished western region of the fishing grounds was instigated in an effort to alleviate pressure on the main known stock. This catch limit was only based on historical catch levels, and acts as an interim measure until appropriate catch levels aimed at minimizing impacts on the octopus stocks can be determined.

Octopus pallidus is a species of medium size (maximum 1.2 kg) endemic to southeast Australian waters, from the Great Australian Bight to central New South Wales, including Bass Strait and Tasmania (Stranks, 1996), and is commonly found at depths of 7–275 m on sandy substrata and in bryozoan gardens (Stranks, 1988). As a terminal spawner, *O. pallidus* produces batches averaging ~400 eggs (Leporati *et al.*, 2008a) and hatchlings that weigh ~0.25 g (Leporati *et al.*, 2007). The average lifespan for *O. pallidus* is ~12 months, although animals older than 18 months have been found (Leporati *et al.*, 2008b). *Octopus pallidus* does not demonstrate any considerable sexual dimorphism and has a potential peak spawning period during late summer and early autumn (Leporati *et al.*, 2008a). In addition, recent work by Doubleday *et al.* (2008a), who investigated the elemental signatures of *O. pallidus* stylets in Tasmanian waters, revealed that the species has highly structured populations and considerably smaller spatial ranges (<85 km) than merobenthic species such as *O. maorum* (>500 km), which was analysed using the same methods (Doubleday *et al.*, 2008b).

This work used the OPF as a case study to assess whether commercial cpue data could be a reliable indicator of stock status for holobenthic octopus fisheries. To achieve this, cpue and biological information from an experimental research line were investigated for consistency in their interpretation of stock status and compared with trends in the commercial fishery cpue. The information was used to estimate the effects of commercial fishing on local octopus stocks, with particular regard to brooding females and recruitment.

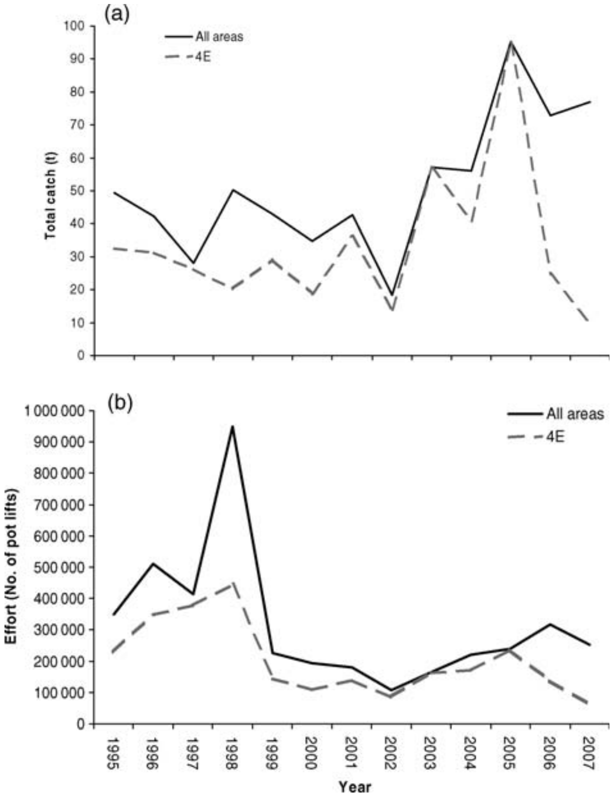

Figure 2. (a) Total annual catch and (b) total number of pot lifts per year (effort) in the OPF during the years 1995–2007 in all areas (solid black line) and from the 4E fishing blocks (dotted grey line).

Material and methods

Commercial data

Commercial fisheries information for *O. pallidus* before 1995 was not examined, because logbook records are considered to be unreliable, and catches of both *O. pallidus* and another octopus species were combined in earlier years. Since 1995, however, monthly logbook recordings detailing haul date, total catch, skipper, vessel, depth, location in half-degree fishing blocks of latitude and longitude, and number of pots for each line have been mandatory. From 2004 on, additional GPS coordinates of individual lines have also been recorded. Generally, only octopuses of marketable size (>250 g) are caught in the OPF, so discarding is negligible.

In November 2004, a commercial sampling programme was introduced to the OPF, in which fishers were required to collect all octopuses caught in 50 randomly selected pots for each line, representing 10% of a standard commercial line. From these 50-pot samples, the total and gutted weight of the catch, numbers of males and females, and percentages of pots with eggs were recorded. In instances where multiple lines were clustered within a 15-km radius, fishers were only required to sample one line.

The total annual catch per fishing block during the period 1995–2007 was mapped to visualize spatial and temporal trends.

The cpue for each record was calculated by dividing the total weight of the catch (kg) by the number of pots per longline used. Soak times lasting 1–83 d showed no significant relationship with catch per pot (regression analysis, $F = 2.897$, $r^2 = 0.003$), so were not included in the calculation of cpue. The weighted mean of seasonal sex ratios derived from the 50-pot samples collected between summer 2004/2005 and spring 2006 were applied to the historical fishery data to determine differences in cpue between males and females.

The cpue data for males and females in the historical main fishing area that has been fished consistently over the years (fishing blocks 4E1, 4E2, 4E3, and 4E4; Figure 3) were standardized with generalized linear models to estimate an index of abundance. The models were fitted with different combinations of various factors for which information was available, viz. fishing location (block), vessel, depth, and season. The effects of individual fishers were fully nested in the vessel factor owing to minimal transfer of skippers between vessels. All fishing gear used in the fishery was consistent between vessels and throughout years and, therefore, was not included in the analysis. Moreover, no significant technological advancements that could have influenced cpue were introduced into the fishery during the period, with GPS and echosounder equipment operating from 1995 on (M. Hardy, pers. comm.).

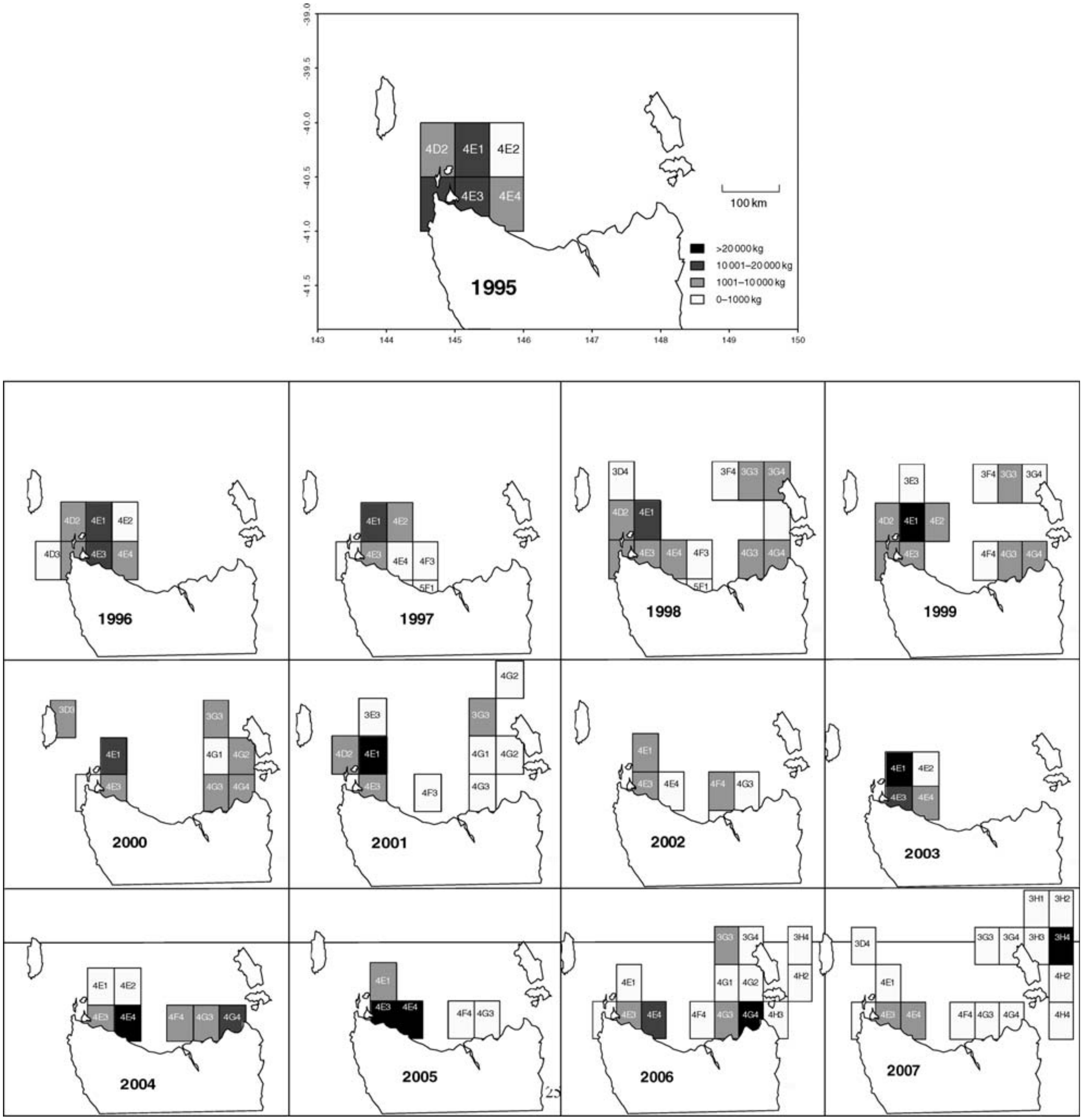

Figure 3. Fishing area and total catch per fishing block for *O. pallidus* for each year, 1995–2007. The block number is given for fishing blocks with catch returns. The legend for 1995 applies to all other maps.

The cpue data were standardized using a stepwise approach, where the factor that best fitted the data was added to the model first and then followed by progressive factors until additional factors failed to improve the fit. Akaike's Information Criterion (AIC; Maunder and Punt, 2004) was used to determine the model with the best fit:

$$\mathrm{AIC} = -2\ln \ell + 2p, \qquad (1)\leftarrow$$

where ℓ is the maximum likelihood function and p the number of parameters.

A surplus production model (Polacheck *et al.*, 1993) was trialled using annual or seasonal data on catch and effort. However, it failed to make any sensible biomass predictions, potentially because of the lack of sufficient contrast in the data and/or high recruitment variability. Instead, standardized cpue data were investigated for intra- and interannual patterns through time-series analysis. Only data from spring 1998 to summer 2005/2006 could be used in the time-series analysis, because this period displayed the most consistent fisheries dynamics with no changes in the fleet or management arrangements. To determine if there were significant differences in cpue between seasons, analyses of variance (ANOVAs) were run for both males and females. Time-series analyses were performed on male and female standardized and detrended cpue data separately, each lag representing 1 year split into quarterly (seasonal) steps. Autocorrelation plots were used to determine any periodicity in cpue data. Significant autocorrelations were further investigated through partial autocorrelation plots, measuring the strength of the correlation at a specific lag and removing the effects of all autocorrelations below that lag. Cross-correlation analyses were used to determine whether any trends in male and female cpue were attributable to mean monthly sea surface temperature (SST) information derived from satellite data downloaded from the US National Oceanic and Atmospheric Administration (NOAA) web page http://las.pfeg.noaa.gov/oceanWatch.

Research line

An experimental research line was deployed by one of the commercial fishing vessels in February 2005 to supplement the historical logbook and 50-pot sample data. The research line was not used to determine the status of the whole stock, but was deployed to provide an indication of the effects of continual fishing pressure in a single location. Sampled every 2 months between April 2005 and November 2006 on 11 independent trips, the research line was 1 km long, consisted of 145 pots, and was fished at the one continuous location (between 40°43.342′S 145°20.060′E and 40°43.788′S 145°20.505′E) at a depth of 26 m. The location of the research line was near the home port of Stanley in the heavily fished block 4E3 within the main historical fishing area (Figure 3). However, no fishing activity had taken place in the exact location and the immediate vicinity of the research line 12 months before setting up the research line. If multiple trips occurred during a single season, the results were pooled. The sex and the total and gutted weights and dorsal and mantle lengths of all octopuses collected from the research line were recorded. This information allowed for occupancy rate to be used in addition to cpue. Reproductive information derived from a study by Leporati *et al.* (2008a) that used the same dataset was applied in the present study. Applications of these data included (i) the estimation of potential fecundity in mature females (ovaries containing eggs) and (ii) determining the number of spawning females. These tasks were carried out by counting the number of eggs in a subsample from the ovary, followed by conducting an ANOVA on egg numbers to determine if there were any significant differences in potential fecundity between seasons, then classifying females as "spawning" if they had eggs ready to lay, denoted by the presence of stalks in either the ovary or oviducts, or if there were eggs in their pots. The software package R was used to perform all analyses except the ANOVAs and regression analyses, for which the software package SPSS was used.

Results

Commercial data

During the period 1995–2001, total catches of *O. pallidus* were consistently between 30 and 50 t year^{-1}. In 2002, catches dropped to 18 t, but increased steadily again during the period 2003–2007, with a peak of 95 t in 2005 (Figure 2a). The number of pots hauled per year (effort) more than doubled in 1998 compared with the previous year, but it then stabilized, but gradually increased from 2002 on (Figure 2b).

Catch and effort during the years 1995–2005 was predominantly focused on the 4E fishing block, which provided reasonably consistent returns throughout the period (Figures 2a, 2b, and 3). The acquisition of a larger vessel with a greater range in 1998 made possible the exploration of fishing grounds farther east. However, a large drop in cpue in 1998 led to a return in 1999 to the use of smaller vessels with reduced range, and the introduction of the limit of 20 000 pots by management authorities. The record catch of 95 t in 2005 from the 4E fishing blocks instigated the introduction of the 100-t local area limit by management. As a result, a larger vessel with a greater range was purchased again in 2006, and fishing operations moved east in 2006 and 2007, to fishing blocks 4G4 and 3H4 off Flinders Island (Figure 3).

Sex ratios in the 50-pot sampling programme displayed significant differences between seasons ($\chi^2 = 402.7$, d.f. = 13, $p < 0.001$). Females were considerably underrepresented in catches during summers of 2004/2005 and 2005/2006 compared with other seasons, whereas in summer 2006/2007, there was a lag in this pattern, females representing a greater percentage of the catch. This was potentially a product of the considerably smaller sample sizes collected after spring 2006 (Figure 4, Table 1). Throughout the sampling period, no significant relationship was found between sex ratios and fishing blocks (regression analysis, $F = 1.565$, $r^2 = 0.009$).

The most influential factor on cpue in the 4E fishing blocks was season followed by fishing block, vessel, and depth (Table 2). The model with the best fit for both males and females contained an interaction term between depth and season (Model 6). The standardized cpue for both males and females was relatively uniform during the period summer 1995–spring 1997, but then dropped substantially between autumn 1998 and spring 1999 (Figure 5). From spring 1998 to summer 2006, there was an increasing trend in female cpue, with significant seasonal ($F = 5.713$, d.f. = 28, $p = 0.023$) fluctuations; every 2 years, there were increasingly high peaks during summer and autumn, with smaller peaks in the years in between. Male cpue also increased during the same period and demonstrated significant seasonal differences ($F = 6.308$, d.f. = 28, $p = 0.018$). However, male cpue was more irregular and had less pronounced 2-year peaks during summer/autumn

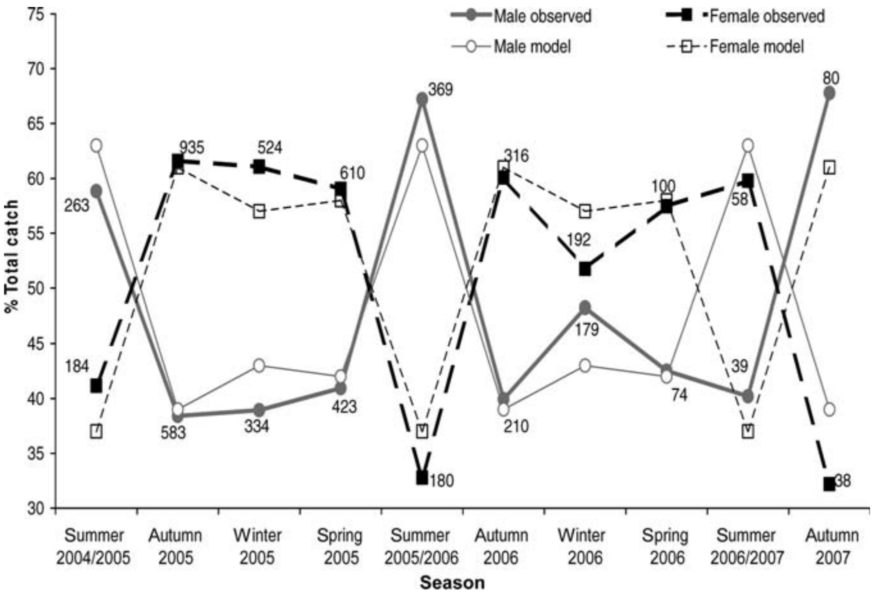

Figure 4. Percentage of male and female *O. pallidus* caught in the 50-pot sampling programme (observed) and used in the catch rate standardization (model). The numbers represent male and female 50-pot sample sizes for each season. The model data are derived from the weighted mean of the observed data for each season.

Table 1. Raw data collected from the commercial fishery 50-pot sampling programme for *O. pallidus*.

Season	Number of lines	Number of pots	Total number of octopuses	Number of males	Number of females	Mean % of pots with eggs	Sex ratio male:female
Summer 2004/2005	18	900	447	263	184	3.5	1:0.69
Autumn 2005	42	2 100	1 518	583	935	8.5	1:1.6
Winter 2005	24	1 200	858	334	524	14.9	1:1.56
Spring 2005	29	1 450	1 033	423	610	13.6	1:1.44
Summer 2005/2006	19	950	549	369	180	6.6	1:0.48
Autumn 2006	24	1 200	526	210	316	5.8	1:1.5
Winter 2006	16	800	371	179	192	5.2	1:1.07
Spring 2006	8	400	174	74	100	12.8	1:1.35
Summer 2006/2007	4	200	97	39	58	10.6	1:1.48
Autumn 2007	3	150	118	80	38	9.3	1:0.47

Table 2. Statistical models compared in the standardization of *O. pallidus* cpue.

		Male			Female		
Model	Description	AIC	d.f.	Adjusted r^2	AIC	d.f.	Adjusted r^2
1	cpue = year + season	−5 037	49	0.51	−4 506	49	0.62
2	cpue = year + season + block	−5 051	52	0.57	−4 522	52	0.63
3	cpue = year + season + block + vessel	−5 061	55	0.58	−4 529	55	0.63
4	cpue = year + season + block + vessel + depth	−5 065	61	0.58	−4 534	61	0.63
5	cpue = year + season + block + vessel + depth + vessel × season	−5 128	81	0.60	−4 585	81	0.65
6	cpue = year + season + block + vessel + depth + vessel × season + depth × season	−5 167	150	0.62	−4 603	150	0.67

Model 1 is the equivalent to the geometric mean of the cpue and acts as a base for the remaining models. Model 6 was the model with the lowest AIC, so was chosen as the best model. The adjusted r^2 and degrees of freedom (d.f.) are provided.

than female cpue. From summer 2006 to winter 2007, the cpue in the 4E fishing blocks for both males and females dropped to substantially lower levels than in previous years. From spring 1998 to summer 2006, summer displayed a strong regular annual fluctuation for both males and females (Figure 6). Catch rates in winter and spring did not show any regular annual pattern, and autumn displayed a similar yet weaker pattern to that of summer.

The time-series autocorrelation identified a 2-year periodicity in the standardized female cpue data between spring 1998 and summer 2006, with a significant positive correlation at a lag of 2 and 4 years (Figure 7a). The partial autocorrelation analysis indicated that the 2- and 4-year trends were independent, i.e. that they did not directly influence each other. The standardized cpue for males was more irregular than for females, but showed similarly

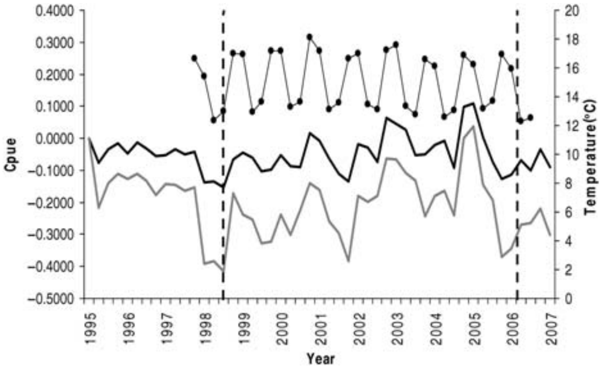

Figure 5. Seasonal standardized cpue for female (line) and male (grey line) *O. pallidus* caught in the 4E1, 4E2, 4E3, and 4E4 fishing blocks between summer 1995 and winter 2007, and the mean SST, 1998–2006 (line with dots). Vertical dashed lines denote the period spring 1998 to summer 2006 used in the autocorrelation analysis.

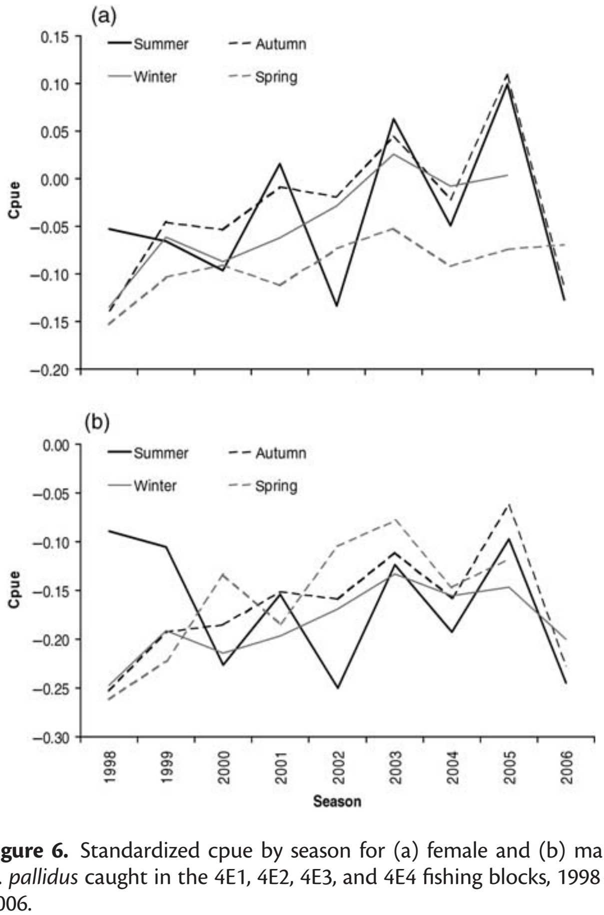

Figure 6. Standardized cpue by season for (a) female and (b) male *O. pallidus* caught in the 4E1, 4E2, 4E3, and 4E4 fishing blocks, 1998–2006.

strong peaks every 2 years. The time-series autocorrelation and partial autocorrelation identified a direct negative correlation between catch rates at a lag of 0.75 years (Figure 7b). The cross-correlation between cpue and SST did not show any significant trends for either females or males (Figure 8), indicating that mean seasonal SST was not a driving factor in the observed cpue periodicity for males or females.

Research line

In contrast to the results of the 50-pot sampling programme, females were much more likely to be captured year-round on the experimental research line. In all, 112 males and 536 females were caught from April 2005 to November 2006. The cpue displayed an initial decline during winter 2005, but then stabilized (Figure 9a). Seasonal occupancy rates for females were relatively consistent, ranging from 38 to 46%, but peaked during autumn, at 62% in 2005 and 66% in 2006. Males were poorly represented in research line catches throughout the sampling period, with occupancy rates ranging from 5% during summer 2005/2006 to 15% during winter 2005. Fecund females were caught throughout the year, with potential fecundity similar between seasons ($n = 80$, $F = 0.915$, d.f. $= 6$, $p = 0.489$). The proportion of fecund females that were spawning declined during the sampling period, until an increase during spring 2006 (Figure 9b). Similarly, mean whole weight decreased over progressive seasons for both males and females caught (Figure 9c). Fecundity displayed a positive linear relationship with whole weight for mature females ($r^2 = 0.42$), smaller females being less gravid. In contrast, fecundity had a minimal relationship with either dorsal or ventral mantle length ($r^2 = 0.0883$ and $r^2 = 1.859$, respectively).

Discussion

Although trends in commercial cpue data did not fully match the results of the experimental research line, both data sources indicated that cpue information alone is an unreliable indicator of stock status for holobenthic species of octopus. Seasonal commercial cpue levels were highest when female sex ratios and brooding periods were at their peaks, suggesting that cpue is strongly influenced by seasonal changes in sex-specific catchability. In contrast to the commercial cpue, no strong seasonal trends in cpue were evident from the experimental research line. Rather, the consistent and concentrated fishing pressure applied to the research line diminished cpue only initially. However, occupancy rates suggested a seasonal pattern in the proportion of spawning females, and mean whole weight for females decreased. As such, even if cpue displays seemingly constant trends, the underlying composition and recruitment potential of the fished octopus populations may be substantially impacted by fishing.

Under the relatively low fishing pressure applied to the research line, cpue and occupancy rates showed little evidence of exploitation. However, the constant localized fishing pressure on the research line demonstrated signs of size-selective fishing mortality, with reductions in the proportion of spawning females and mean whole weight for females. The positive relationship between whole weight and fecundity in females suggested that size-selective fishing mortality may have had an impact on future recruitment. The lack of any relationship between length data and fecundity was expected, owing to the absence of any rigid structures in cephalopods from which a reliable length measurement can be made (Jackson *et al.*, 2000). Regardless of any relationships, no significant reductions in mean female fecundity were demonstrated in the research line. This may be attributed to the use of underdeveloped eggs in the fecundity analysis and, therefore, to egg reabsorption rates not being accounted for.

The decline in the proportion of spawning females and mean weight of both sexes is unlikely to be a result of strong recruitment of small animals or the emigration of large ones. Smaller females

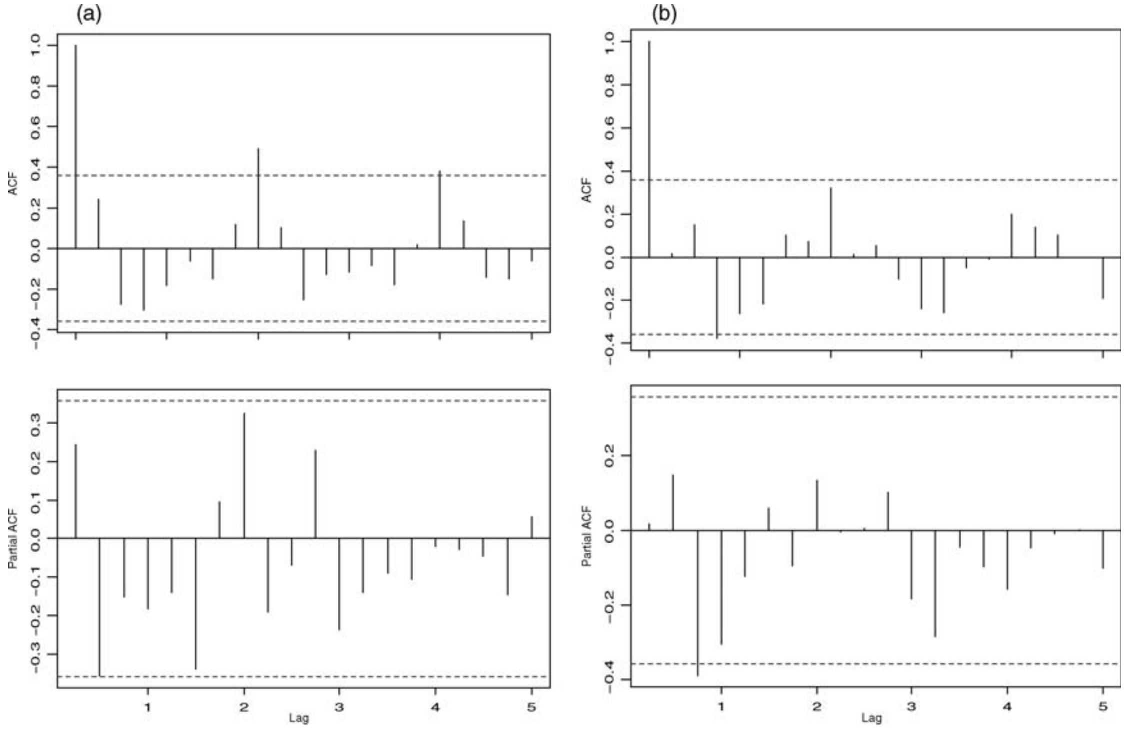

Figure 7. Autocorrelation and partial correlation plots of the standardized cpue for seasonal catches of (a) female and (b) male *O. pallidus*, with 5% significance levels (dotted lines). ACF denotes the autocorrelation function, and the lag is equal to 1 year, with quarterly (seasonal) increments.

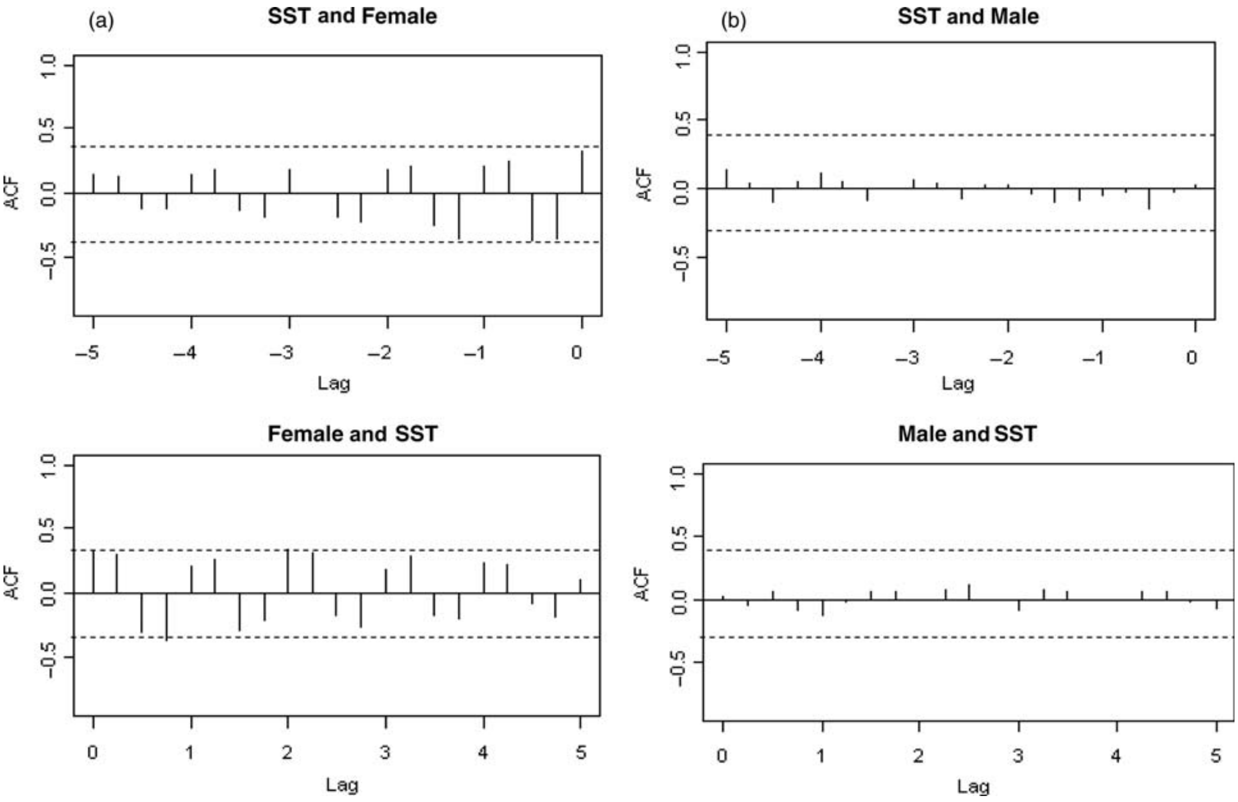

Figure 8. Cross-correlation analysis of the standardized mean cpue for seasonal catches of (a) female and (b) male *O. pallidus* and mean seasonal SST, with 5% significance levels (dotted lines).

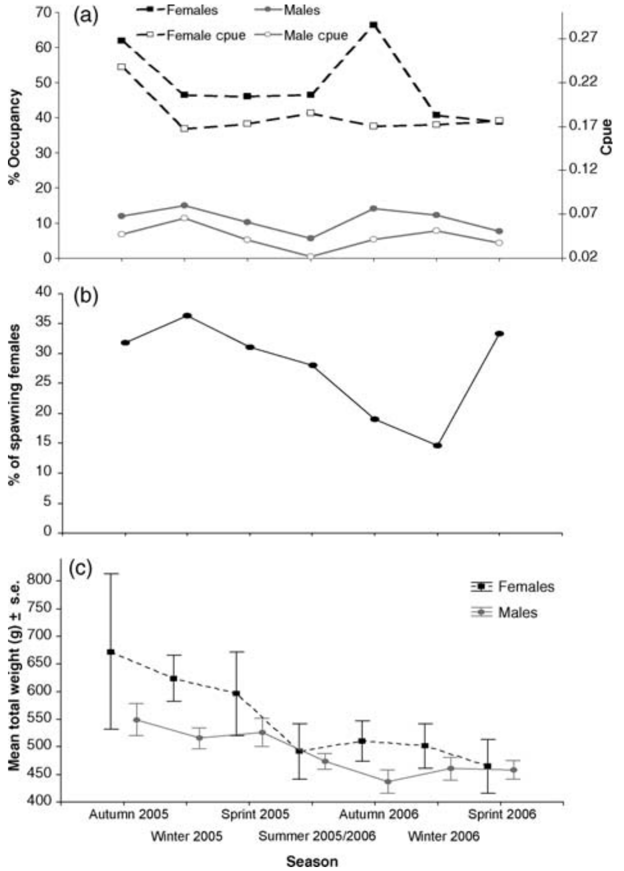

Figure 9. *Octopus pallidus* (a) percentage occupancy and the cpue of males and females, (b) proportion of spawning females, and (c) mean total weight of females and males caught on the research line by haul-season. Multiple trips during single seasons have been pooled.

have a competitive disadvantage when competing for appropriate brood sites in a habitat-limited environment, and tend not to replace larger females who spend more time in pots while brooding eggs. Whereas emigration of large octopuses may have contributed to the consistently decreasing mean weights, this would require an increase in emigration rates over the fishing period to match the observed trends. Evidence of size-selective fishing mortality in the same dataset was also given by Leporati *et al.* (2008b), female weight-at-age decreasing and growth increasing with subsequent sampling seasons. Therefore, the consistent and concentrated fishing pressure on the research line led to the progressive removal of larger, more fecund, older, and slower-growing females, with smaller, less fecund, younger, and faster-growing females subsequently replacing them. Although the population biomass may be compensated to some extent by this higher productivity of octopuses, sustained high fishing pressure could severely reduce egg production and subsequent recruitment, as proposed by Rodhouse *et al.* (1998). Such impacts of fishing on the population are not necessarily detectable in cpue data until a later stage, when cpue strongly fluctuates (Hampton *et al.*, 2005; Maunder *et al.*, 2006). Here, the commercial cpue appeared to be much influenced by female vulnerability, although it remained unclear whether other factors (e.g. different habitat structure or levels of exploitation rates) were responsible for the strong variation in the seasonal patterns of cpue (or the lack thereof) between the commercial operations and the research line. As a result, a reliance on cpue information could also lead to further misinterpretation and positive abundance bias attributable to pots functioning as potential aggregation devices in the habitat-limited sandy substrata and attracting octopuses from farther afield. This has particular relevance for females, which are reliant on finding suitable structures to brood eggs (Anderson, 1997).

Females were especially vulnerable to exploitation during autumn in each year from 1998 to 2006, with elevated cpue levels and large proportions of females then. High catches of females during autumn are likely linked with females actively seeking shelter to brood eggs (Iribarne, 1990; Anderson *et al.*, 2002). The length of time *O. pallidus* broods its eggs is unknown, but temperature is a defining factor for brooding duration in other octopus species (Caverivière *et al.*, 1999). Although *O. pallidus* spawns throughout the year, a potentially optimal spawning period during late summer and early autumn has been identified by Leporati *et al.* (2008a). The autumn cpue peak and the optimal spawning period were not completely aligned. However, optimal spawning periods are strongly influenced by environmental conditions, have fluid time frames, and can shift in intensity from year to year (Silva *et al.*, 2002; Fernández-Rueda and García-Flórez, 2007). This suggests that the vulnerability of brooding females to fishing pressure varies throughout the year, with the greatest potential for fishing pressure to adversely affect egg production being during the optimal spawning period (Faraj and Bez, 2007).

Over a period of 7 years (1998–2006), the commercial cpue showed marked gender-specific intra- and interannual periodicity patterns that were strongly influenced by season. These seasonal patterns were not directly related to mean monthly SST, although water temperature influences growth (Forsythe, 1993), reproductive development (Forsythe and Hanlon, 1988), and metabolic rate in cephalopods (Katsanevakis *et al.*, 2005). The lack of a direct link between SST and cpue emphasizes the importance of other seasonally variable factors, such as recruitment, food availability, behaviour, and the movement and migration of genders at different temporal and spatial scales (Gillespie *et al.*, 1998).

From 1998 to 2006, female cpue generally increased, with successively higher peaks in summer and autumn every 2 years. This interannual trend could be aligned with the general 12-month lifespan of *O. pallidus* (Leporati *et al.*, 2008b). Although the partial autocorrelation analysis showed no evidence of time-lagged density-dependence, this pattern may have been confounded by environmental fluctuations (Ambrose, 1988; Faure *et al.*, 2000). Male cpue displayed a less regular pattern than female cpue, but also showed strong peaks every 2 years. The negative influence of cpue in one season on the season 0.75 years later could be caused by density-dependent factors such as food availability or cannibalism. However, to obtain a better understanding of this phenomenon, further study on the seasonal distribution and abundance of *O. pallidus* juveniles that recruit to the fishery at around 250-g body weight is required. Further research is also needed on the distribution and abundance of *O. pallidus* in habitats, such as bryozoan, sponge, and ascidian gardens, compared with the habitat-limited sandy substrata utilized by the fishery. Such information would help determine whether the catchability of octopus is lower in more complex habitats and if distinct habitats are utilized by different life stages.

The cpue in the 4E fishing blocks declined when fishing operations were moved to eastern Bass Strait in 2006. However, it remained unclear whether the drop in cpue and the assumed decline in abundance was a direct consequence of the previous record catches in 2005, or whether lower cpue was the result of altered fishing practices attributable to effort being concentrated in the east. Independent of the cause, shifting fishing effort 300 km to eastern Bass Strait would have relieved all pressure on the western population. Differences in elemental signatures of *O. pallidus* stylets have indicated that octopus from the 4E fishing block may form separate and possibly unconnected populations from those in eastern Bass Strait off the east coast of Flinders Island (Doubleday *et al.*, 2008a). Different *O. pallidus* populations could also exist at much smaller scales (0<85 km; Doubleday *et al.*, 2008a), which would mean that the OPF covers several distinct populations. Small distances between unconnected populations of holobenthic species of octopus are not uncommon. Narvarte *et al.* (2006) demonstrated that recruitment for the holobenthic species *Octopus tehuelchus* can vary between sites 22 km apart. In contrast, the merobenthic *O. vulgaris* showed no significant differences in microsatellite DNA markers within 200 km (Cabranes *et al.*, 2008). Such differences in population structure, which are most likely related to factors such as the extent of movement and migration, hatchling dispersal, the effects of geographic features and oceanic processes, and the availability of suitable habitats (Boyle and Boletzky, 1996; Semmens *et al.*, 2007), underscore the point that holobenthic and merobenthic species of octopus require management strategies that are adapted to their specific spatial population dynamics.

For holobenthic species, it is important to prevent localized depletion by distributing effort over a wide area. The eastern and western Bass Strait regions currently used to manage the OPF are too large to achieve this goal. Rather, annual catch limits should be based on smaller spatial units, e.g. half-degree fishing blocks. As a precautionary approach, it should be assumed that the drop in cpue in 2006 was caused by overexploitation of the octopus populations in 2005, so the actual limit per fishing block should be less than the 2005 single block maximum. The small number of operators in the OPF at present would allow for self-regulation of fishing block catch limits. However, if effort increases considerably and is shared by a number of operators, it could be regulated during the peak spawning period in autumn on a rotational basis between different fishing blocks, to ensure that impacts during this period are spread throughout the fishery and between populations.

Our study has demonstrated that cpue data should be combined with biological information to estimate the impacts of fishing on the populations of holobenthic octopus species. Changes in the reproductive potential and subsequent recruitment caused by continual fishing pressure on localized populations may potentially remain undetected in commercial fisheries data. To avoid such situations, holobenthic octopus fisheries need to be managed on smaller scales than merobenthic species, and cpue data need to be accompanied by size, sex, and reproductive information. To avoid potential impacts on recruitment, it is proposed that management of the OPF be operated at the smaller spatial scale of individual fishing blocks.

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